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Vesicular–Arbuscular Mycorrhizae of Some Hawaiian Dune Plants[1]

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ABSTRACT: The mycorrhizal status of dune plants from the island of Hawaii was investigated. All plants, including *Batis maritima*, *Cocos nucifer*, *Ipomoea brasiliensis*, *Pennisetum setaceum*, *Prosopis pallida*, *Scaevola taccada*, and *Sporobolus* sp., had vesicular–arbuscular mycorrhizae (VAM). Levels of colonization by VAM fungi ranged from less than 10% to 100% of the root length and were highest in *Ipomoea*, *Pennisetum*, and *Sporobolus*. Twelve species of VAM fungi were recovered, half of which are undescribed. The most frequently recovered species were *Sclerocystis sinuosa*, *Glomus microaggregatum*, an undescribed *Glomus* sp., and an undescribed *Scutellospora* (*Gigaspora*) sp. The composition of the VAM fungal communities of the black sand dunes differed from those of the quartz and carbonate dunes. The community of Hawaiian dune mycorrhizal fungi was very distinct from dune communities of Australia, San Miguel Island (California), the Atlantic Coast of the United States, Scotland, and Italy. The presence or absence of VAM fungi in dunes may have been of critical importance to the successful colonization of the Hawaiian Islands by some vascular plants, and these fungi may thus have influenced the subsequent development of the native flora.

THE IMPORTANCE OF vesicular–arbuscular mycorrhizae (VAM) in the establishment and growth of sand dune-colonizing plants was first suggested by Nicolson in 1959. Since that time, the role of VAM fungi in alleviating the effects of low soil phosphate and water stress on plants in a variety of habitats has been well documented (e.g., Harley and Smith 1983). Sand dune soils appear to be especially favorable to development of VAM because of their low phosphorus content (Koske and Halvorson 1981, Ranwell 1972), and VAM appear to be required for significant sand dune stabilization to occur (Koske and Polson 1984). VAM have now been identified from maritime and lacustrine dunes in numerous temperate locations, including the continental United States (Bergen and Koske 1984, Friese 1984, Koske 1987, Koske and Halvorson 1981, Koske and Tews 1987, Sylvia 1986, Tews and Koske 1986), Canada (Koske et al. 1975), Scotland (Nicolson 1959, 1960, Nicolson and Johnston 1979), and Italy (Giovannetti 1985, Giovannetti and Nicolson 1983). VAM also have been reported from maritime dunes of subtropical Australia (Jehne and Thompson 1981, Koske 1975).

In addition to benefitting the host plant directly through improved phosphate nutrition and indirectly by reducing water stress (e.g., Huang et al. 1985), VAM fungi contribute to stabilization of sand dunes by binding sand grains into larger aggregates and improving soil structure (Clough and Sutton 1978, Forster and Nicolson 1981, Koske et al. 1975, Sutton and Sheppard 1976). Such improved soil structure is significant in influencing plant succession on the dunes, which occurs as they age (Nicolson 1960, Olson 1958, Ranwell 1972).

Previous studies of VAM in sand dunes have concerned those associated with continents. The unusually large size of VAM fungal spores (up to 1 mm diameter) restricts their dispersal by wind in comparison to other fungi, and these one-celled propagules may not survive as long in the upper atmosphere

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as do multicellular structures. Additionally, the remoteness of the Hawaiian Islands from large land masses that could serve as a source of VAM fungi and the relatively young age of the islands (30 million years for the oldest members of the chain) are important factors in limiting the number of species of VAM fungi introduced. Spores of VAM fungi that did arrive on these islands had to be deposited near living roots for the colonization to be successful because VAM fungi are obligate symbionts. Since VAM fungi may be intimately involved in primary colonization of sand dunes (Koske and Polson 1984), and because a significant number of colonizations of the Hawaiian Islands by vascular plants occurred in beach and dune habitats (Carlquist 1974), it was of interest to determine the mycorrhizal status of some dune-inhabiting plants of Hawaii and to compare the composition of the VAM fungal community to those occurring in sand dunes in other localities.

MATERIALS AND METHODS

Soil samples (approx. 500 ml) were collected from the root zones of plants growing on dunes or the upper beach at four sites on the island of Hawaii on 17–18 July 1984 and 19–22 July 1985 (Figure 1). Sites were selected to permit sampling of different sand types and localities and included black volcanic sand dunes at Kaimu (Kalapana) and Punaluu, quartz sand dunes at Hapuna State Beach, and a mixed quartz and carbonate dune on the western edge of the old Kona Airport north of Kailua. Soil samples were stored in plastic bags at room temperature for 3 weeks and then at 5°C for an additional 3 weeks until processed. Spores from the 1984 collections were recovered from the soil by filtration (Koske and Walker 1984) and from the 1985 collections by wet-sieving/sucrose centrifugation (Walker et al. 1982). Every spore that appeared viable (intact and with cytoplasmic contents) was removed from the filter paper, mounted on a slide in a polyvinyl alcohol solution (PVLG) (Koske and Tessier 1983), crushed, and identified using a compound microscope at 400–1000 ×. Species of VAM fungi were identified by comparison with type or validated specimens. Terminology used in the descriptions of spores follows the standards recommended by Walker (1983, 1986) and Morton (1986).

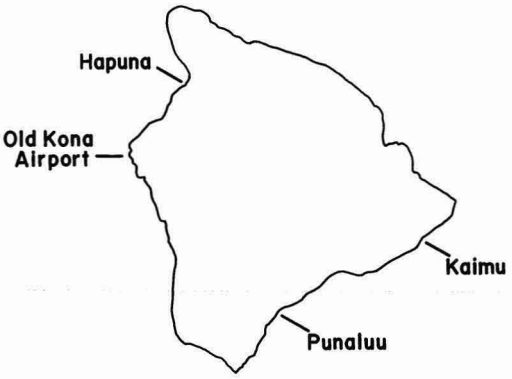

FIGURE 1. Collection sites on the island of Hawaii.

Root samples were collected from dunes at Hapuna State Beach and near the old Kona Airport (Kailua) on 17–18 July 1984. Root fragments were stored in soil for 3 weeks at room temperature before being fixed in FAA (formalin/acetic acid/alcohol). Fixed roots were stained to assess mycorrhizal development by a modification of the technique of Phillips and Hayman (1970). Roots were cleared by autoclaving for 3 min in 10% KOH, rinsed in water, suspended in a weak HCl solution (10 ml conc. HCl/1 liter H_2O), and stained in a lactic acid/glycerol/water (1 : 2 : 1) solution containing 0.05% trypan blue (wt./vol.). Roots were autoclaved for 3 min in the trypan blue solution and destained by autoclaving for 3 min in a lactic acid/glycerol/water solution lacking trypan blue. If roots were still dark after treatment in KOH, they were placed in 10% Clorox bleach (=0.525% NaHOCl) until straw yellow (Bevege 1968) and then were suspended in the dilute HCl solution and treated as described above. Extent of VAM colonization was determined by estimating to the nearest 10% the length of root system containing arbuscules, vesicles, hyphal coils, or internal hyphae.

Soil pH was measured in a 1:2 soil:0.01 M $CaCl_2$ slurry (Schofield and Taylor 1955)

after a 30-min equilibration. The pH values were converted to their arithmetic equivalents before they were averaged (Daubenmire 1947). Chloride was measured by immersing an Orion chloride electrode (model 97–16) in a slurry of soil and 50 ml of deionized water containing 1 ml of an isotonic salt solution (4.3 M $NaNO_3$). Chloride readings (in milligrams per kilogram) are expressed on a dry weight basis. Sand grain size classification was determined by passing soil samples through a series of U.S. standard soil sieves (10, 18, 35, 60, and 140 mesh). Field capacity was estimated by measuring the amount of water retained after saturated soil samples were allowed to drain for 4 hr.

RESULTS AND DISCUSSION

The finest sand occurred at the Hapuna Beach site, and the coarsest sands were those from the black sand beaches (Figure 2). Field capacities of the sites reflected the differences in soil particle size (Table 1). Chlorides varied from an average of 427 mg/kg at the Kaimu site to 2096 mg/kg at Punaluu. Variation between samples from the same site was great, as indicated by the large standard deviations. Soil pH ranged from 6.6 at Kaimu to 7.6 at Hapuna Beach.

Roots of all seven species of plants were colonized by VAM fungi (Table 2). Levels of colonization ranged from <10% in a *Pen-*

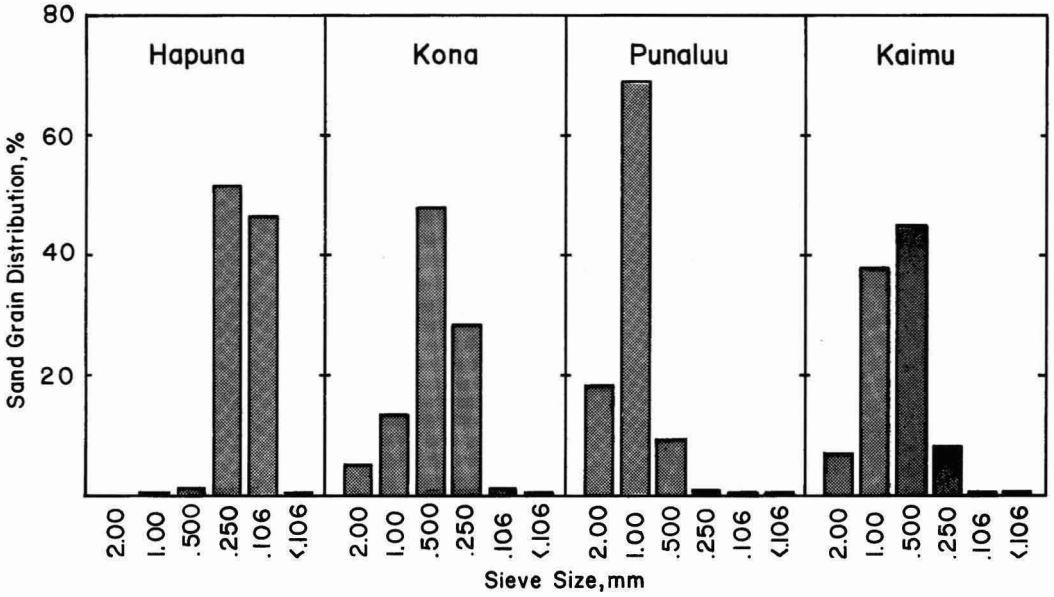

FIGURE 2. Sand grain size distribution of the four collection sites.

TABLE 1

SOME PHYSICAL CHARACTERISTICS OF FOUR HAWAIIAN DUNE SITES

	HAPUNA	KONA	PUNALUU	KAIMU
pH	7.6 ± 2.6*	7.3 ± 3.8	6.9 ± 4.5	6.6 ± 1.5
Chlorides (mg/kg)†	880 ± 298	642 ± 448	2096 ± 2348	427 ± 106
Field capacity	27.6 ± 1.7	27.4 ± 2.7	18.1 ± 0.1	17.2 ± 8.6

*Mean ± standard deviation (SD).
†Calculated as milligrams Cl per kilogram of soil (dry wt./dry wt.).

TABLE 2

EXTENT OF VAM DEVELOPMENT IN SOME HAWAIIAN DUNE PLANTS

HOST SPECIES	PERCENT COLONIZATION*
Hapuna Beach	
Ipomoea brasiliensis (L.) Sweet	60, 90
Prosopis pallida (Willd.) HBK	60
Sporobolus sp.	80, 90
Old Kona Airport	
Batis maritima L.	50
Cocos nucifer L.	50
Ipomoea brasiliensis	100
Pennisetum setaceum (Forsk.) Chiov.	90, 40, < 10
Scaevola taccada (Gaertn.) Roxb.	50, 30, < 10

* Percent of root length of individual plants colonized by VAM fungi.

nisetum plant near the old Kona Airport to 100% in an *Ipomoea* plant growing at the same site. The average percent infection for all plants sampled was 61%. Some of the root systems were heavily colonized by mycorrhizal fungi (Figures 3–6), especially the roots of *Ipomoea*, *Pennisetum*, and *Sporobolus*. *Batis* roots were lightly colonized, and few vesicles or arbuscules were present. *Batis* typically grows in marshy sites (Hillebrand 1888), habitats generally unfavorable to formation of extensive mycorrhizae (Gerdemann 1968). The development of VAM in *Cocos* roots was not especially dense, but in some areas of the roots the cortical cells were filled with hyphal coils (Figure 6) and arbuscules, and 50% of the root system was colonized.

A study of vascular plants growing on Heron Island of the Great Barrier Reef (Peterson et al. 1985) revealed high levels of VAM development in both *Scaevola taccada* and *Sporobolus virginicus* (L.) Kunth that were growing on the strand. In that study, no attempt was made to isolate or identify spores of associated VAM fungi.

Of the 12 species of VAM fungi recovered from the Hawaiian dune soils and listed below, 50% could not be assigned to described species and are thought to be new species. These are referred to in the text by my collection number (e.g., *Glomus* 807). Enough material was obtained to attempt pot cultures with three of the undescribed species, and these will be formally described when sufficient spores have been harvested.

1. *Acaulospora scrobiculata* Trappe (1977)

Figure 7

Spores were recovered only from two samples collected from the root zones of coconut trees at Kaimu. This species is readily recognized by the surface ornamentation and arrangement of the spore walls. Spores of *A. scrobiculata* have been frequently isolated from sand dunes in southeastern Australia (Koske 1975) and in the Atlantic coast dunes of the United States (Bergen and Koske 1984, Koske 1987, Koske and Halvorson 1981, Tews and Koske 1986). The species is also known from sand dunes of Lake Michigan (Koske and Tews 1987) and the Bahamas (Koske, unpublished data).

2. *Entrophospora* 838

Figures 8, 9

Spores are pale yellow to golden brown in transmitted light, globose to irregular in shape, measure 70–100 × 70–140 μm, and are produced on a hyphal terminus (Figure 8) characteristic of the genus (Ames and Schneider 1979). The spore wall structure consists of five walls: Wall 1 is colored, minutely pitted, and measures 2–3 μm thick. Walls 2–5 are hyaline membranous walls, measuring

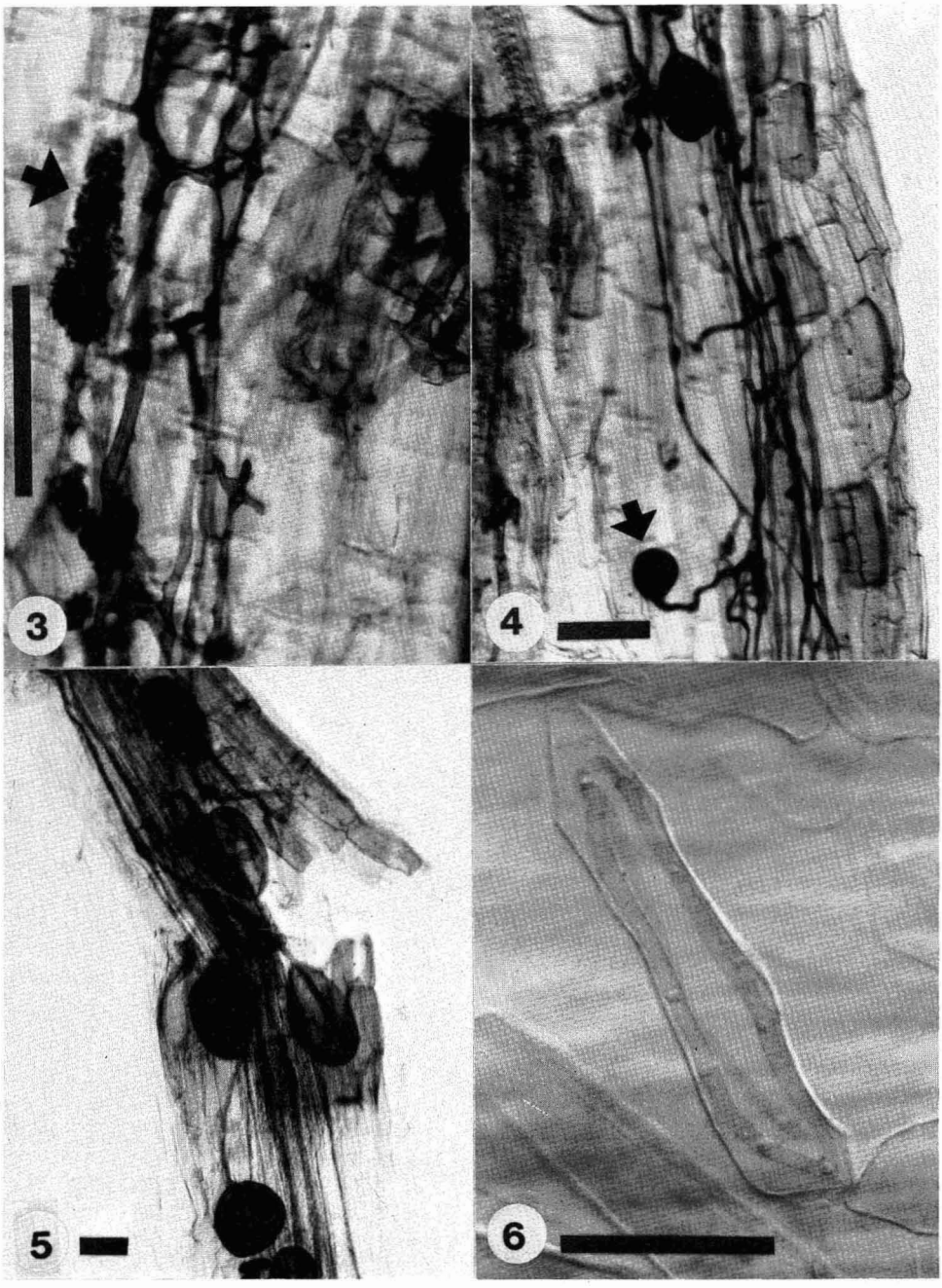

FIGURE 3–6. Stained roots with VAM fungi. 3, *Scaevola taccada*: note arbuscule (arrow) and hyphae; 4, *Ipomoea brasiliensis*: note dark-staining VAM hyphae and vesicles (arrow); 5, *Pennisetum setaceum* with vesicles; 6, *Cocos nucifer* cortical cell with VAM hyphal coil. (Bar = 50 μm.)

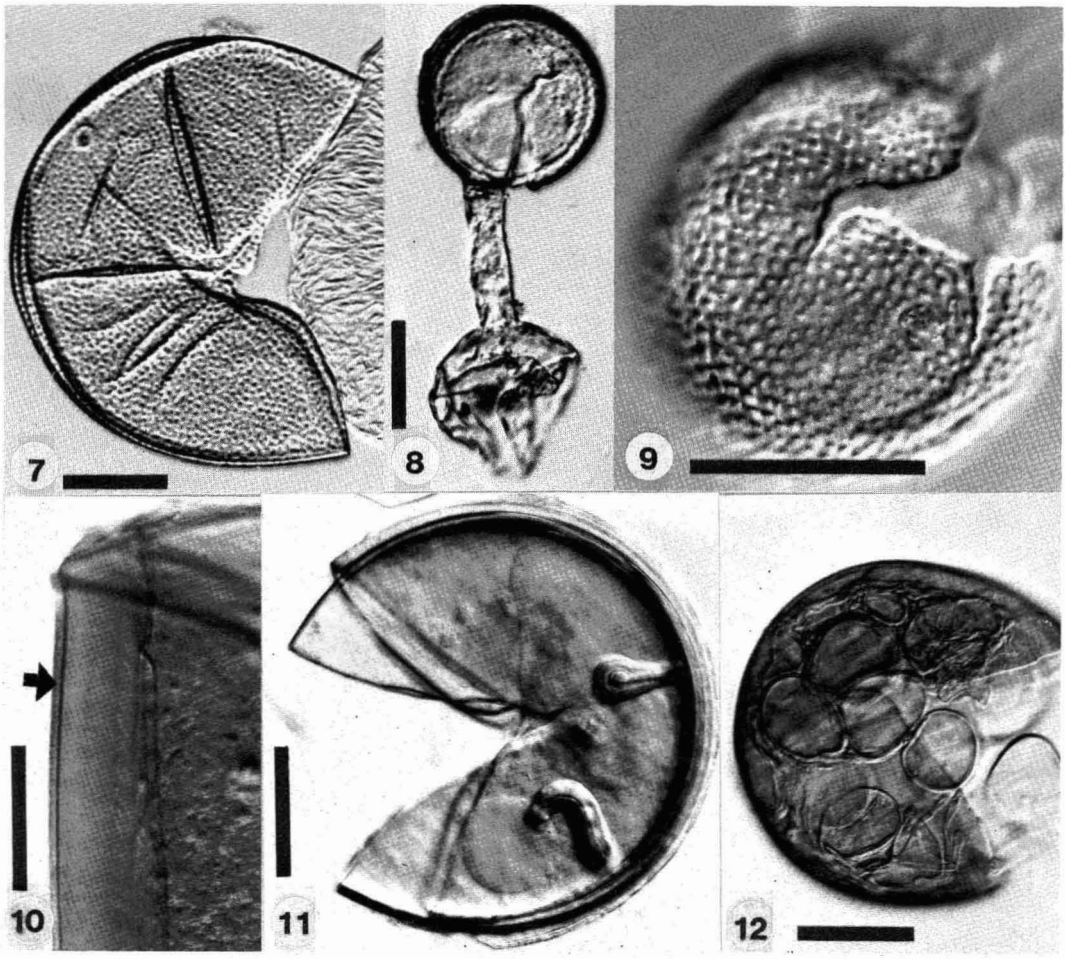

FIGURE 7–12. Spores of Hawaiian VAM fungi. 7, *Acaulospora scrobiculata*: note pitted surface; 8, 9, *Entrophospora* 838: 8, spore attached to hyphal terminus; 9, surface of spore with prominent pits; 10, *Gigaspora* 807: note thin outer wall (arrow) and thick, laminated inner wall; 11, *Glomus intraradices*: spore wall is coarsely laminate, note lignituberlike ingrowths, probably produced in response to microbial attack; 12, spores of *Glomus microaggregatum* inside dead spore of *Glomus* 807. (Bar = 50 μm.)

0.5–1.2, 1–1.8, 0.6–1.2, and 0.8–1.2 μm thick, respectively. Wall 4 has a beaded appearance, a feature often noted in spores of some *Entrophospora* and *Acaulospora* species (Morton 1986, Schenck et al. 1984, Trappe 1977). The pitting on the outer spore wall of *Entrophospora* 838 is very similar to that on the spores of *A. scrobiculata*.

Spores were recovered from a single collection from the root zone of an unidentified grass growing in the swale behind the main dune at Punaluu. Chloride at this site was very high, measuring 4805 mg/kg. This soil had a water holding capacity of 18%. Thus, plants growing in this soil at field capacity would experience a chloride concentration of 21,622 mg/kg, approx. 17% greater than seawater.

3. *Gigaspora* 807

Figure 10

Spores formed singly in the soil, orange-brown to reddish-brown, globose, 360–480 μm diameter. Spore wall structure of two

walls: Wall 1 a unit wall, pale yellow, smooth, 2–2.5 μm thick, closely appressed to wall 2. Wall 2 laminated, yellow-brown to orange-brown, 8–17(–32) μm thick. Suspensorlike cell 40–45 μm diameter, pale yellow-brown. Auxiliary cells not observed.

Spores of this species were infrequently recovered, occurring in only three samples. Occasional dead spores were occupied by other species of VAM fungi. The species was found in association with *Scaevola* and *Ipomoea*. Insufficient material was obtained to attempt pot cultures.

4. Glomus aggregatum Schenck & Smith (1982)

This species is a common inhabitant of sand dunes of the eastern coast of North America and the Great Lakes (Koske 1985, 1987) and occurs on San Miguel Island in California's Channel Islands National Park (Koske, unpublished observations). It was present in one sample of *Scaevola* from Hapuna Beach and one sample of *Batis* from the Kona Airport site. Huang (1987) previously reported the species from Hawaii associated with introduced plants in nondune sites.

5. Glomus constrictum Trappe (1977)

This species was recovered from a single collection beneath *Pennisetum* at the Kona Airport site. The characteristic dark color of the spores and the branching of the subtending hypha were diagnostic. *Glomus constrictum* has been reported from dune sites on the Atlantic coast of the United States (Koske 1987), and occurs in agricultural soils on the west coast of the continental United States (Nemec et al. 1981, Trappe 1977).

6. Glomus intraradices Schenck & Smith (1982)

Figure 11

This was the fourth most frequently recovered species, occurring in 21% of the samples. Spores occurred freely in the soil and inside dead spores of *Scutellospora* 816. The multiple walls of the spore separate easily when spores are crushed. It was recovered from root zones of *Scaevola*, *Ipomoea*, *Batis*, and an unidentified grass. The species occurs in nondune soils on San Miguel Island, but has not been found in dune soils there (Koske, unpublished observations).

7. Glomus microaggregatum Koske, Gemma, & Olexia (1986)

Figure 12

Spores of this species were recovered from 38% of the samples, typically occurring inside dead spores of other *Glomus*, *Gigaspora*, or *Scutellospora* species. This species is common in sand dunes of the Atlantic coast of the United States (Koske et al. 1986) and is present on San Miguel Island (Koske, unpublished observations). *Glomus microaggregatum* occurred in association with *Scaevola*, *Ipomoea*, *Pennisetum*, *Batis*, *Cocos*, and *Sporobolus*. This was the smallest-spored VAM fungal species isolated from Hawaiian dunes (15–40 × 15–50 μm).

8. Glomus 803

Figure 13

Spores formed in tight clusters (sporocarps). Spores pale yellow, globose, subglobose, ovoid to irregular, 23–50 × 25–42 μm. Spore wall structure composed of a single laminated wall 1.5–2.5(–4) μm thick. Subtending hypha concolorous with spore, 5–7 μm thick, frequently breaking off just below the point of attachment to leave an apiculate scar. Thickness of wall of attachment hypha 3 μm at spore base, soon tapering to <1 μm below attachment. Pore open or closed by a septum.

Spores occurred in a single sample collected from the root zone of *Scaevola* at Kona. This undescribed species has recently been found in desert soils in Arizona (C. Walker, personal communication)

9. Glomus 807

Figure 14

Spores orange-brown to reddish brown, globose to subglobose, 72–150 × 80–170 μm. Spore wall structure consisting of two walls:

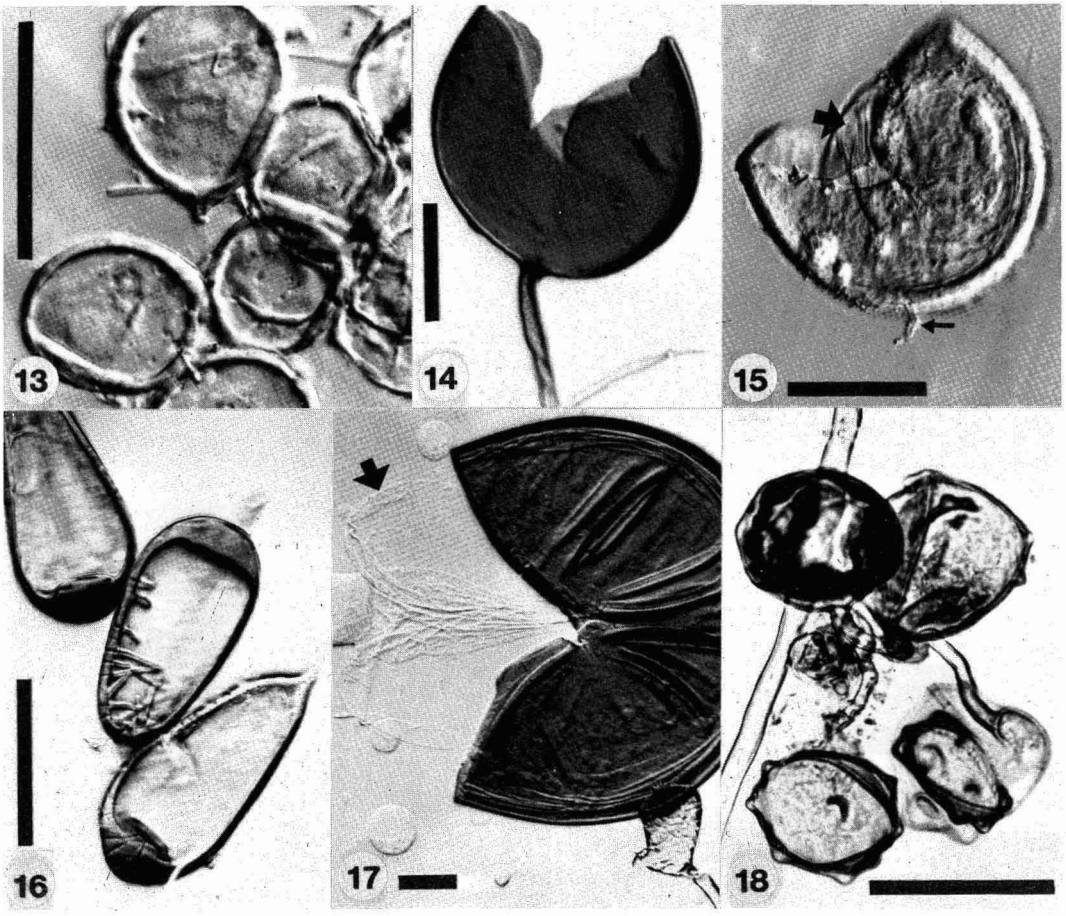

FIGURE 13–18. Spores of Hawaiian VAM fungi. 13, *Glomus* 803; 14, *Glomus* 807; 15, *Glomus* 840: note small attachment hypha (small arrow) and innermost spore wall (large arrow); 16, *Sclerocystis sinuosa*: note lignituberlike ingrowths in the center spore; 17, 18, *Scutellospora* 816: 17, crushed spore with innermost amorphous wall extruded (arrow); 18, auxiliary cells produced on coiled hyphae. (Bar = 50 μm.)

Wall 1 hyaline to pale yellow, sloughing off and frequently absent, 0.5–2 μm thick, closely appressed to wall 2. Wall 2 orange-brown to red-brown, laminated, 4–8 μm thick. Subtending hypha yellow-brown to orange-brown, constricted, recurved or straight at spore base, 5–7 μm wide at point of attachment, up to 12 μm at widest point if constricted. Walls 1–2 μm thick. Spores often have a collar on the inner side of wall 2 adjacent to the attachment hypha, similar to that present in *G. deserticola* Trappe, Bloss, and Menge (1984). Small specimens were very similar in appearance to *G. deserticola*, but differed in having thicker spore walls and in the generally larger spore dimensions.

Glomus 807 was the third most frequently recovered VAM fungal species (33%) and was present in all sites. It occurred in association with *Scaevola*, *Ipomoea*, *Pennisetum*, *Cocos*, and *Batis*.

10. Glomus 840

Figure 15

Spores hyaline to very pale yellow, globose, 60–80(–100) μm diameter, formed singly in the soil. Spore wall structure of two walls in

one group: Wall 1, 5–8 μm thick, often encrusted with debris. Wall 2 a coriaceous type of wall, 1–3 μm thick. Subtending hypha hyaline, 3–6 μm broad, often difficult to observe. Wall thickness of subtending hypha 1–1.2 μm.

Glomus 840 occurred only in samples from *Cocos* from the Kaimu dunes.

11. Sclerocystis sinuosa Gerd. & Bakshi

Figure 16

This species occurred in 33% of the samples. Its sporocarps were especially common in samples from Hapuna and Kona, and were associated with *Scaevola*, *Cocos*, *Pennisetum*, *Ipomoea*, and *Batis*. *Sclerocystis sinuosa* has been reported from both Asia and western North America (e.g., Gerdemann and Bakshi 1976, Nemec et al. 1981).

12. Scutellospora 816

Figures 17, 18

Spores formed singly in the soil on a bulbous suspensorlike cell. Spores globose to pyriform, orange-brown, 200–310 × 215–360 μm. Spore wall structure consisting of four walls: Wall 1 orange-brown, 1.5–3(–5) μm thick. Walls 2 and 3 closely appressed hyaline unit walls. Wall 2, <0.5 μm thick, brittle, with radial fissures in crushed spores. Wall 3, 1–1.5 μm thick. Wall 4 an amorphous type of wall of variable thickness, greatly wrinkling in polyvinyl alcohol mountants (Figure 17) and staining reddish purple in Melzer's reagent. The amorphous wall of this species has the same features as were originally described for this wall type from several *Acaulospora* species by Morton (1986). When spores are examined in an acid mountant such as PVLG, the thickness of this wall is dependent upon the pressure applied to the coverslip. Suspensorlike cell attached terminally or sublaterally, yellow-brown, 50–65 μm broad, with walls measuring 1–4 μm thick. Auxiliary cells (Figure 18) orange-brown, formed singly or in clusters of 4–6, borne on coiled hyphae. Individual cells are ornamented with knobby projections and are 40–55 μm broad.

Scutellospora 816 occurred in 38% of the samples and was especially abundant at Hapuna Beach. Spores were recovered from the root zones of *Scaevola*, *Ipomoea*, *Pennisetum*, *Cocos*, and *Sporobolus*. The coarse orange-brown hyphae and similarly colored auxiliary cells of this species also were present in soil samples from which no spores were recovered.

This species formerly would have been placed in the genus *Gigaspora* Gerd. & Trappe, but that genus was recently split into two genera, *Gigaspora* and *Scutellospora* (Walker and Sanders 1986).

The frequency of occurrence of VAM fungal species at each collecting site is shown in Table 3. Comparisons of the differences in composition of the fungal community between sites must be drawn cautiously because of the differences in plant species sampled at each site and the low number of samples collected at Punaluu and Kaimu. Nevertheless, certain species were recovered with significantly greater frequency at some sites than at others. These included *Acaulospora scrobiculata*, which occurred significantly more frequently at Kaimu (50%) than at Kona (0%). This species also was absent from the two other sites, but its absence was not statistically significant (because of the small number of samples from those two sites). Similarly, *Scutellospora* 816 was significantly more frequent at Hapuna Beach (82%) than at Kona (29%), and *Sclerocystis sinuosa* was significantly more frequently recovered at Kona (57%) than at Hapuna (9%).

More species of VAM fungi were recovered from the sites on the western side of the island than on the eastern side. In part, this reflects the greater number of samples collected on the western side, but three species (*Sclerocystis sinuosa*, *Gigaspora* 807, and *Scutellospora* 816) that were routinely isolated from Hapuna and Kona were absent from Punaluu and Kaimu. *Glomus intraradices* also was more prevalent on the western side. These differences may result from the coarseness of the soil of black sand dunes and associated edaphic factors rather than from differences in host plants, since *Cocos* and *Scaevola* were common to both the western and eastern sampling areas.

The average species richness (number of species per root zone) of VAM fungi for the 39

TABLE 3

FREQUENCY OF OCCURRENCE (PERCENTAGE) OF VAM FUNGI AT FOUR DUNE SITES

SPECIES	HAPUNA ($n = 11$)	KONA ($n = 21$)	PUNALUU ($n = 3$)	KAIMU ($n = 4$)	ALL SITES ($n = 39$)
Acaulospora scrobiculata	0*AB†	0 AB	0 A	50 B	5
Entrophospora 838	0	0	33	0	3
Gigaspora 807	18	5	0	0	8
Glomus aggregatum	9	5	0	0	5
G. constrictum	0	5	0	0	3
G. intraradices	27	19	33	0	21
G. microaggregatum	64	33	33	0	38
Glomus 807	45	33	33	0	33
Glornus 803	5	0	0	0	3
Glomus 840	0	0	0	100	10
Sclerocystis sinuosa	9 A	57 B	0 A	0 A	33
Scutellospora 816	82 A	29 B	0 AB	0 AB	38

*0 = absent

† Frequencies in rows followed by the same letter do not differ significantly ($p > 0.05$). Frequencies not followed by letters do not differ from other values in that row. Data from Punaluu and Kaimu were combined for statistical analysis because each had too few collections to be analyzed separately.

samples was 2.4. Highest average richness occurred at the Hapuna Beach site (3.3), followed by Kaimu (2.3), Kona (2.1), and Punaluu (1.7). The absolute number of VAM fungi recovered from individual root zones ranged from 0 to 6. Maximum VAM fungal richness in a single root zone of different host species was: *Batis* (5), *Cocos* (3), *Ipomoea* (4), *Pennisetum* (4), *Scaevola* (4), *Sporobolus* (2).

The average richness in Australian dunes varied from 1.5 in foredunes to 2.4 in second dune ridges (Koske 1975). Richness was slightly greater (3.1) in Rhode Island dunes (Koske and Halvorson 1981). A survey of VAM fungal activity along a 355-km-long temperature gradient in Atlantic coast dunes from New Jersey to Virginia (Koske 1987) revealed a significant correlation between increasing average temperature and richness. Richness at the northern end of the study area averaged 4.2 and increased to 6.3 at the southern limit. The lower richness observed in the Australian and Hawaiian sites may actually reflect the presence of fewer species, seasonal fluctuation in spore abundance (Gemma 1987), or the result of the presence of nonsporulating or infrequently sporulating species. Sporulation by VAM fungi has frequently been observed to correlate with cessation of root growth in temperate climates (e.g., Saif 1977, Sutton and Barron 1972). Thus, a favorable climate for year-round root growth may inhibit sporulation of VAM fungi or favor those species with reduced ability to sporulate (Baylis 1969).

Another factor that could account for the lower richness in the Hawaiian samples was losses of spores to parasitism by other soil microorganisms. Janos (1980*a*) noted similar high losses to parasitism in Costa Rican soils. Most soil samples in the present study contained more dead than live spores. The spores of *Sclerocystis* (Figure 16) and *Glomus intraradices* (Figure 11) frequently bore lignituber-like ingrowths similar to those noted in other species (Khan 1971, Koske 1985, Mosse 1956, Mosse and Bowen 1968).

Five of the 12 species of VAM fungi recovered from sand dunes of Hawaii in the present study have not previously been reported elsewhere. Whether these species are endemic cannot be determined until more areas of the earth are examined for VAM fungi. The composition of the VAM fungal community of Hawaiian dunes differed markedly from that reported for other maritime dune systems. On the U.S. Atlantic coast, species of *Gigaspora* and *Scutellospora* predominate, and 29 species have been recovered there (Bergen and Koske 1984, Friese 1984, Koske

1987, Koske and Halvorson 1981, Sylvia 1986, Tews and Koske 1986), 4 of which were present in the Hawaiian dunes. Sand dunes of San Miguel Island, California, are dominated by several undescribed species of *Glomus* and *Scutellospora* and by *Glomus pansihalos* Berch and Koske (Koske, unpublished observations); only *Glomus aggregatum* and *Glomus microaggregatum* are shared with the Hawaiian dune mycoflora. Dunes in New South Wales, Australia, were characterized by an undescribed *Glomus* species (red-brown laminate spores), 2 *Scutellospora* species (not present in Hawaiian dunes), and *Acaulospora scrobiculata* (Koske 1975). In dunes in Queensland, Jehne and Thompson (1981) found spores of *Scutellospora calospora* (Nicol. and Gerd.) Walker and Sanders and *Glomus fasciculatum* (Thaxter sensu Gerd.) Gerd. & Trappe. Italian sand dunes contained spores of several species of *Glomus* and *Scutellospora* not found in Hawaiian dunes, and none of *Acaulospora* or *Entrophospora* (Giovannetti 1984, Giovannetti and Nicolson 1983). Maritime dunes in Scotland contained only a single VAM fungal species, *Glomus fasciculatum* (Nicolson and Johnston 1979).

In tropical rain forests in Costa Rica, different plant communities resulted when cleared areas were revegetated, depending on the occurrence of VAM fungi in the soil (Janos 1980*b*). Success of plant species in these sites was determined largely by their mycorrhizal dependency. Obligately mycotrophic species (those requiring VAM to complete their life cycle) were not present in the VAM-free sites, although they dominated in the sites where VAM fungi were present in the soil. Similarly, for many of the plant species that arrived as seeds or vegetative fragments on Hawaii's shores, the presence or absence of VAM fungi in the dunes may have been of critical importance in determining the success of each potential colonization. These early successes or failures thus had profound effects on the development of the island flora. The uniqueness of the Hawaiian flora (94% of the native vascular plants are endemic) attests to the infrequency of successful colonizations (Carlquist 1980). While it generally has been assumed that failed colonizations are the result of the failure of seedlings or vegetative portions of new arrivals to establish because of abiotic conditions at a particular site, it is possible that some failures result from the inability of invading species to establish mycorrhizae because of the absence of mycorrhizal fungi from the site. Clearly, obligately mycotrophic species cannot become established until VAM fungi are present. It would be of interest to examine the mycorrhizal dependency of Hawaiian plants and to reexamine the origin of the Hawaiian flora (including the phenomena of disharmony and fruit and seed gigantism) from a mycorrhizal viewpoint.

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